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SEX RECOGNITION AMONG AMPHIPODS.¹

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How do males of the amphipod crustacea distinguish the females? It is well known that the males of the Gammaridea have the curious habit of carrying the females under their body for a considerable time. This act of transportation has probably no further significance in relation to the fertilization of the eggs than to secure the proximity of the two sexes when the proper time for fertilization arrives. According to the observations of Della Valle on *Gammarus pungen* the eggs are not fertilized until after they are laid, oviposition occurring a short time after moulting. When the moulting of the female has been effected, the male bends his body beneath that of his mate and deposits spermatozoa upon the ventral surface of her thorax. The deposit of sperm is followed within half an hour by the laying of the eggs. After the act of copulation the male regains his original position and swims about with the female as before. The same relation of oviposition to moulting was found by Miss Langenbeck in *Microdeutopus*, the male leaving the female during her moulting process but soon resuming his previous position when the moult was completed.

The instinct of the male amphipod to seize and retain hold of the female is one of remarkable strength. The male retains his hold, despite all efforts to dislodge him, with remarkable persistence, and will still cling to the female after the posterior half of his body has been cut away. My own observations on the sexual behavior of amphipods relate mainly to three species, *Amphithoe longimana* Smith, *Hyalella dentata* Smith and *Gammarus fasciatus* Say. The sexual behavior of these three species is remarkably similar, although they belong to as many distinct families. The female while being carried about keeps remarkably impassive. Her thoracic legs are drawn up, the abdomen held strongly flexed, the whole body assuming as compact a form as possible. She takes little or no part in swimming; the movement of the

¹ From the Zoölogical Laboratory of the University of Michigan, Ann Arbor, Mich.

pleopods when the body is strongly bent upon itself serves only to keep a current of water passing by the gills. She is carried about like a helpless burden, allowing her vigorous spouse to assume the entire labor of transportation and the responsibility of keeping her as well as himself out of danger. The efforts of the male to seize the female and get her into the proper position to be carried have the effect of inducing her to throw herself into the characteristic bodily attitude and remain quiet. The attitude assumed by the female is similar to that observed in the ordinary thigmotactic reaction of amphipods and may, perhaps, be but the same form of response, somewhat modified and specialized in relation to the function of reproduction. When the males are torn away from the females they soon seize their partners again and roll them about into the proper position and then proceed on their way in apparent contentment. The female as soon as seized by the male curls up and allows herself to be rolled and tumbled about without a show of resistance or protest. The males, as a rule, are considerably larger than the females and usually get their partners into the desired position quite readily ; but when a small male attempts to carry a large female he experiences much difficulty. I have observed a male *Hyaella* endeavoring to carry a female somewhat larger than himself. After seizing the female he would turn her around until she finally came into the proper position for transportation, but owing to the larger size of his partner the male could not reach around her body so as to carry her away. No sooner was the female properly adjusted than the male would lose hold of her round body and the same efforts had to be repeated. During all this performance the female remained dutifully passive. After watching the further struggles of the male for over half an hour I became convinced, although he was not, that he had undertaken an impossible task, and discontinued my observations.

In order to ascertain if sight plays any part in sex recognition in *Hyaella*, I tore some males away from their partners, blackened their eyes with asphalt varnish, and placed them in a dish with several females. It was not long before each of the blinded males was provided with a mate. Sight, therefore, is not the determining factor in sex recognition in this species.

That the females are distinguished through the sense of smell seemed more probable, since it has been shown that among many insects sex recognition is brought about in this way. The sense of smell in crustaceans is often highly developed and in some groups probably affords the means by which the females are distinguished. The sense of smell in the crustacea is mainly, although not quite exclusively,¹ located in the first antennæ. To determine if the male distinguishes the other sex by this sense, recourse was had to the experiment which naturally suggested itself, of removing the first antennæ of several males and observing whether they experienced any difficulty in finding mates. It was found that after they had recovered from the slight shock of the operation, the males seized the females as eagerly as before and carried them about in the usual manner. Even after both pairs of antennæ were removed the females were seized and carried in the same way. It is very improbable, therefore, that the sense of smell plays an important part in enabling male *Hyaell*as to distinguish the other sex. The experiment was then tried of placing several females in a small enclosure of wire gauze, while several males which had recently been torn from females were placed in the same dish, but outside of the enclosure. The males paid not the slightest attention to the females within the gauze; but soon after the gauze was raised and the females allowed to scatter through the dish most of the males had acquired a partner.

If one attentively observes *Hyaell*as as they are swimming about, it will be seen that the males do not pursue the females, great as their eagerness may be to seize and carry one of the opposite sex. Only when the two sexes collide in their apparently random movements does the male become aware of the presence of the female. When a male and a female collide, the female curls up and lies quiet while the male makes efforts to seize her. Should two females collide, they may curl up for a moment, but as they are not seized they soon pass on. When two males meet there is often a lively struggle. Each apparently attempts to seize and carry the other, but as neither will consent to remain passive they soon separate. The different reactions of the two sexes to

¹ Bethe, *Archiv. mic. Anat.*, Bd. 2, 1897; Holmes, *Biol. Bull.*, Vol. II., 1901.

contact with other individuals is the factor which effects the union of the males with the females. Each reacts to the reactions of the other. The male has a strong instinct to seize and carry other individuals of the same species. The female has the instinct to lie quiet when another individual comes into contact with her, especially if she is seized. The instinctive reactions of the two sexes are complementary and coöperate to bring about and maintain the peculiar sexual association characteristic of the Gammaridea. If the association of the sexes is brought about by their peculiar modes of reaction to certain contact stimuli, it would seem probable that the only reason why males do not carry other males as well as females is that they are prevented from so doing by the active resistance of their intended mates. I was accordingly led to try the experiment of mutilating some male specimens so that they could no longer make effective resistance to seizure. The large second gnathopods (the principal means of defense) of several males were cut off and the mutilated individuals were placed in a dish with several males which were recently torn from females. The mutilated males were soon seized and carried about as if they were members of the other sex. In one case a mutilated male was carried about for over five hours. The mutilated males were more active than females are under the same conditions, and did not assume the same bodily attitude, but nevertheless their captors carried them without any manifest awareness of the deception to which they were subjected.

Male *Hyaell*as, however, will not carry dead specimens of either sex, at least for more than a short time. I have observed males of both *Hyaella* and *Gammarus* struggling for a time with a dead specimen, but their efforts to carry it were soon discontinued. The failure to carry dead individuals may be due to odor or some sort of chemical stimulation from the object seized, or to the lack of an occasional movement causing a struggle on the part of the male to retain his hold. Stimuli of the latter kind may be necessary to cause the instinctive reaction of the male to continue.

There can be little doubt that the origin of the instinct of the male amphipod to seize and carry the female is to be sought in a modification of the act of copulation. The lower crustacea af-

ford many cases in which the association of the two sexes is prolonged for a considerable period. The males of *Artemia* clasp the females with their peculiarly modified antennæ and the two sexes swim about together for several days (Leydig). Among the free-swimming copepods the male may continue clasping the female for some hours after, as well as before, depositing the spermatophore (Jurine, von Siebold). And among the Cumacea Dohrn has observed the males swimming about upon the backs of the females, much as in Amphipoda. The tendency for the association of the sexes greatly to exceed the act of copulation is apparently quite widespread among the crustacea ; and although, so far as is known, the mating instinct of the Gammaridea is much the same throughout the group so that we cannot trace the successive steps in its development, the sexual behavior of some of the lower crustacea presents many features which may serve to throw some light upon its origin.